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MASS/LENGTH RESIDUALS: MEASURES OF BODY CONDITION OR GENERATORS OF SPURIOUS RESULTS?

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Abstract. In studies of animal ecology, it is fashionable to use the residuals from an ordinary least squares (OLS) linear regression of body mass against a linear measure of size (the body size indicator, BSI) as an index of body condition. These residual indices are used to study the relationship between condition and reproductive investment, survivorship, habitat use, and other parameters. I identify a series of key assumptions underlying the use of this method, each of which is likely to be violated in some or all studies. These assumptions are: (1) that the functional relationship between mass and BSI is linear; (2) that condition is independent of BSI length; (3) that BSI length accurately indicates structural size; (4) that there is no correlation between the size of BSI relative to other structural components (i.e., shape) and the parameter against which the residuals are analyzed; (5) that BSI length is strictly independent of mass; and (6) that BSI length is not subjected to error. Violations of these assumptions place the results of some studies in question and explain the poor relationship observed between OLS residuals and more direct measures of condition.

I use avian morphometric data to illustrate how OLS methods can easily lead to Type I and Type II errors through violations of assumptions (5) and (6). Significant relationships reported between OLS residual indices and parameters correlating with body size (e.g., size of sexual ornaments or egg size) are at particular risk of being spurious when the correlation coefficient between mass and BSI is low. Residual indices of condition are often likely to be more reliable when calculated with alternative methods such as nonparametric or model II regression. However, whatever the method used to produce them, residual indices are not suitable for studying the heritability of condition.

Key words: avian morphometry; body mass; body size indicator; heritability; linearity; nonparametric regressions; reduced major axis; regression method; residual indices of body condition; statistical artifact; structural size.

INTRODUCTION

Body condition is an important determinant of an individual animal's fitness, and its implications are of great interest to ecologists. Many authors have addressed the relationship between condition and ecological parameters such as reproductive investment, survivorship, parasite loads, or investment in characters used in sexual display (e.g., Table 1). Most authors are not explicit about what they mean by ''body condition,'' but they are usually referring to the relative size of energy stores compared with structural components of the body.

Measuring body condition in live vertebrates is a difficult task, and numerous nondestructive methods have been used that are based on relating body mass to linear measures of body size (for reviews, see Blem 1990, Brown 1996). The principal aim of these methods is to separate aspects of body mass that are due to structural size from aspects that reflect fats and other energy reserves. Simple ratios between mass and a linear measure of body size (hereafter referred to as the length of the body size indicator, BSI) have been used by some authors (e.g., Møller 1987, Chastel et al. 1995, Brinkhof 1997, Mateo et al. 1998, Whitfield et al. 1999). Severe problems with ratio methods have already been identified (Blem 1984, Ranta et al. 1994, Jakob et al. 1996), and I do not address them further in this article. In recent years, it has become fashionable to use the residuals of an ordinary least squares (OLS) linear regression of mass against BSI length as an index of condition. It has been argued that such residuals provide the cleanest way to separate the effects of condition from the effects of body size (Reist 1985, Krebs and Singleton 1993, Jakob et al. 1996).

I conducted a literature review of articles published since 1990 that use residual indices as a measure of body condition (Table 1). Undoubtedly, some articles have been overlooked, but the review shows how OLS residual indices are being used in a wide range of important studies of amphibians, reptiles, birds, and mammals published in *Ecology* and other high-quality journals. Authors place considerable faith in the accuracy of these residuals, typically naming them ''body con-

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TABLE 1. Summary of studies since 1990 using residuals from OLS linear regression as a condition index.

Species	Authors	BSI†	*r*	Parameters
Treefrog	Murphy (1994)	TFL		chorus tenure (+)§
Tortoise	Keller et al. (1997)	log SCL		speed (+)§, season§
Lizard	Bradshaw and De'ath (1991)	log SVL	0.98	season§, weather§
Lizard	Dunlap and Mathies (1993)	log SVL		disease (−)§
Adder	Madsen and Shine (1993)	SVL		mass loss§
Python	Shine and Madsen (1997)	log SVL		reproductive threshold§, food supply (+)§
Python	Madsen and Shine (1999)	log SVL		reproductive threshold§, clutch size (+)§, egg size (+)§, year§
Chamaeleon	Cuadrado (1998)	log SVL	0.91‡	mate guarding
Iguana	Wikelski and Trillmich (1997)	log SVL		size§
Spoonbill	de le Court et al. (1995)	$(tars)^3$		plasma chemistry (+)§
Vulture	Kirk and Gosler (1994)	PC1	0.45–0.64	season§, density (−)§
Kestrel	Tella et al. (1997)	$(wing)^3$		nest switching
Pheasant	Mateos and Carranza (1996)	$(tars)^3$		spur length (+)§
Bustard	Carranza and Hidalgo (1993)	log tars		sex trait development, age
Skua	Hamer and Furness (1993)	PC1		aggression§
Owl	Pietiäinen and Kolunen (1993)	arm	0.53	season§, clutch size (+)§, laying date (−)§, hatch success
Swift	Tella et al. (1995*a*)	$(wing)^3$		louse fly abundance
Swift	Tella et al.(1995*b*)	$(wing)^3$		age (+)§
Swallow	Møller (1991)	tars		survivorship
Martin	Christe et al. (1998)	tars		immune response (+)§
Chough	Blanco and Tella (1997)	$(wing)^3$		nest location
Chough	Blanco et al. (1997)	PC1	0.41–0.63	feather mite no. (+)§
Dipper	Ormerod and Tyler (1990)	log wing or tars	0.09–0.77	habitat use§, season§
Flycatcher	Pärt (1990)	tars	0.28	natal dispersal
Flycatcher	Potti and Montalvo (1991)	$(tars)^3$		natal dispersal, hatch date
Flycatcher	Linden et al. (1992)	tars		survivorship (+)§
Flycatcher	Potti (1993)	$(tars)^3$		egg size (+)§
Flycatcher	Schluter and Gustafsson (1993)	tars		clutch size (+)§, heritability§
Flycatcher	Merilä (1996)	tars		brood size (−)§, heritability§
Tit	Lindén et al. (1992)	tars		survivorship (+)§
Tit	Merilä and Wiggins (1995)	tars		survivorship (+)§
Tit	Dufva (1996)	$(tars)^3$		egg volume
Sparrow	Veiga (1993)	tars		badge size (+)§
Sparrow	Møller et al. (1996)	ster		bursa of Fabricius
Sparrow	Cordero et al. (1999)	tars		badge size (+)§
Widowbird	Andersson (1992)	3 log tars		tail length (+)§
Badger	Woodroffe (1995)	log HBL		implantation date (+)§
Squirrel	Dobson (1992)	PC1	0.54–0.85	elevation§
Squirrel	Dobson and Michener (1995)	PC1	0.71	neonate mass§, litter mass§, litter size, parturition date, age
Squirrel	Dobson et al. (1999)	ZAB	0.46–0.58	litter mass§, litter size, juvenile mass, age§

Notes: In each study, body mass was regressed on the body size indicator (BSI). Any transformations are listed, as are values of the correlation coefficient *r* given for the regression (also equal to OLS slope/RMA slope).The residuals were analyzed in relation to the parameters shown. None of these studies includes a comparison of residual indices with more direct measures of condition. Two studies using OLS polynomial regression (Hochachka and Smith 1991, Weatherhead et al. 1995) are not listed.

† Abbreviations: TFL, tibiafibula length; SCL, straight carapace length; SVL, snout–vent length; tars, tarsus; ster, sternum; HBL, head and body length; ZAB, zygomatic arch breadth; PC1, first principal component.

‡ Value not cited in the publication, but provided by the author, *personal communication*.

§ A statistically significant relationship was reported ("+" or "−" indicates sign of the correlation with residual indices). Type I errors are relatively easy to imagine in cases in which the parameter is likely to be correlated with structural size.

dition" without any direct evidence that they are correlated with the size of energy stores.

Here, I provide the first detailed review of these condition indices and achieve three objectives. First, I identify key assumptions underlying the use of OLS residuals as an index of body condition. Second, I show that these assumptions are easily violated and that mass/length residuals may often be an unreliable index of condition, potentially leading to Type I (rejection of a correct null hypothesis) or Type II (acceptance of a false null hypothesis) errors. Third, I identify and evaluate alternatives to OLS residual indices.

ASSUMPTIONS ABOUT LINEARITY

Although there is an apparent consensus in the literature about the appropriateness of OLS linear re-

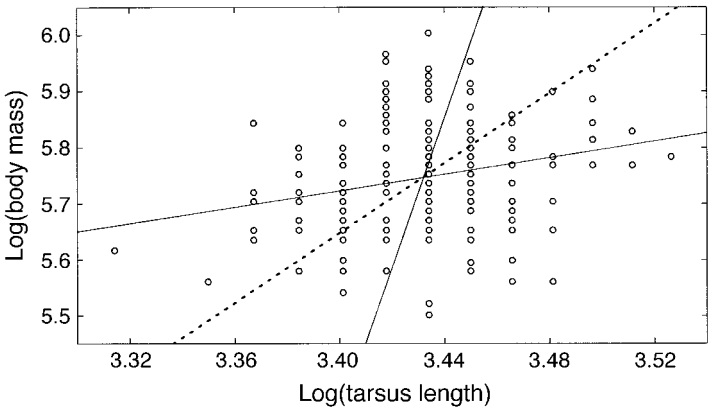

FIG. 1. Lines fitted with different regression methods to a plot of body mass (g) against tarsus length (mm) in male Green-winged Teal (N = 198). The steeper solid line is the OLS regression of X on Y, the shallower solid line is the OLS regression of Y on X, and the central dotted line is the RMA regression.

gression to produce residuals of mass against BSI length, there are major differences between authors in the choice of transformations of mass and BSI length (Table 1). Log transformations are often used on the assumption that body mass = kL^n, where L is BSI length and k and n are constants (and n, the allometric exponent, is equal to the slope of the regression line on a log–log plot). When log transformations are not used, many authors regress mass on BSI^3 (Table 1), implicitly assuming an allometric exponent of three, as expected under a simple geometric model.

The decision to use linear regression of mass on BSI length to produce a residual index of condition makes the assumptions (1) that mass increases linearly with BSI length (following any transformations), and (2) that true condition (i.e., the proportion of body mass made up of energy stores) is independent of BSI length. These assumptions justify the attempt to remove the effect of body size from body mass, yet they are not mentioned or tested in most studies.

Of the studies listed in Table 1, only Pärt (1990) refers to a test of assumption 1 (linearity) in his data. There is no a priori reason why the functional relationship (sensu Rayner 1985) between Y (mass) and X (BSI length) has to be linear. Even after transformation, the linearity assumption is clearly violated in some reptiles (Wikelski and Trillmich 1997), and at the interspecific level in mammals (Silva 1998). This suggests that nonparametric regression methods such as the cubic spline or locally weighted regressions (LOWESS) may be the most appropriate way of producing residual indices in many cases, although this has never been done (for details, see Schluter 1988, Trexler and Travis 1993 for details). Silva (1998) provides an example of applying LOWESS to the mass/length relationship in mammals. These methods make no assumptions about the shape of the functional relationship, and have several advantages over the traditional polynomial methods used by some students of condition (Hochachka and Smith 1991, Weatherhead et al. 1995), particularly in the case of condition indices where the main aim is not to test the significance of the fitted regression model, but rather to find the least biased manner of generating residuals (Schluter 1988, Trexler and Travis 1993).

Assumption 2 is more difficult to test, and violations of this assumption are more problematic. Body condition might well vary with size in animal populations, because size might easily influence foraging success, competition for food, etc. (Schluter 1988, Thessing and Ekman 1994). Weatherhead and Brown (1996) showed how inaccurate residual indices can be when true condition correlates with BSI length, and found that the relative size of fat stores can decrease with body size in snakes. In such circumstances, mass/BSI residuals are poor indicators of condition, because the residuals ideally should not covary with body size (see Weatherhead and Brown 1996: Fig. 1). Although Jakob et al. (1996) argued that the main advantage of OLS residual indices is that they do not vary with BSI length, this is actually an important limitation, as they do not vary with BSI length even when condition does. In such cases, residuals may remain an index of body mass for a given size, but any influence of true condition on ecological parameters under study may be manifested more via a relationship with BSI length than via one with the residuals. The only way to circumvent such problems is to use destructive methods to study condition, such as direct measurements of energy stores (Weatherhead and Brown 1996).

ASSUMPTIONS ABOUT THE RELATIONSHIP BETWEEN THE BSI AND STRUCTURAL SIZE

The reliability of mass/BSI residuals as an index of condition is also heavily dependent on the assumption (3) that the BSI is an accurate measure of overall structural size. As the correlation between BSI length and true size decreases, so will that between the residuals and true condition. In fact, BSI lengths are often weakly correlated with other size measures, largely reflecting variation in shape between individuals of a given size. For example, tarsus, wing, and other measures are weakly correlated with each other or with skeletal mass or volume in adult birds (Wishart 1979, Moser and

Rusch 1988, Rising and Somers 1989, Freeman and Jackson 1990, Merilä and Gustafsson 1993, Gosler et al. 1998). Shine et al. (1997) used mass/snout–vent length (SVL) OLS residuals as an index of ''body shape'' in young pythons. A positive mass/BSI residual for an individual animal may therefore indicate a relatively low BSI length for a given structural size, instead of a relatively high mass for a given structural size.

Thus, use of mass/BSI residuals as a condition index also makes the assumption (4) that there is no correlation between the size of the BSI relative to other structural components (i.e., shape) and the parameter against which the residuals are analyzed. No previous authors (Table 1) have mentioned this assumption, which may be violated in some cases. For example, under directional or fluctuating selection, significant effects of mass/BSI residuals on nestling survivorship (Hochachka and Smith 1991, Lindén et al. 1992, Merilä and Wiggins 1995) could potentially reflect natural selection on relative tarsus or wing size (i.e., shape) rather than an influence of ''physical condition.''

These problems are particularly serious for heritability studies. I suggest that, whatever the regression method used, residual indices are not an appropriate method for studying the heritability of condition. Schluter and Gustafsson (1993) and Merilä (1996) used residuals from a simple OLS regression of mass on tarsus length to study the heritability and underlying variation in the size of subcutaneous fat reserves in nestling flycatchers. Independently of the additional problems arising from the use of OLS regression where there is considerable variation (r between mass and tarsus = 0.28, according to Pärt 1990), heritability of a residual index may reflect heritability of the relative size of the BSI (i.e., tarsus length relative to the overall structural size, shown to be heritable by Merilä and Gustafsson 1993). Other nondestructive methods such as fat scores, breast muscle thickness, and/or TOBEC, total body electrical conductivity (Scott et al. 1995, Winkler and Allen 1996, Gosler et al. 1998) could be appropriate alternatives for studying the heritability of condition.

Because of variation in the relative size of the BSI between sexes or age classes, mass/BSI residuals can be confounded with sex or age (Ormerod and Tyler 1990). Residual indices should therefore be calculated separately for different sexes and age classes where possible. Wing length and other plumage characters should be used as BSIs with particular caution, because these are particularly plastic characters that may covary with season (Rising and Somers 1989, Ormerod and Tyler 1990, Fox et al. 1992) and may not be independent of condition (Pehrsson 1987).

Violations of assumptions 3 and 4 are less likely in those studies using PC1 from a principal components analysis (PCA) of many linear measures (Table 1), which is likely to be a more reliable indicator of structural size (Iskjaer et al. 1989, Freeman and Jackson 1990, Piersma and Davidson 1991).

Assumptions of OLS Methods

Despite the consensus in the literature in the choice of OLS methods to produce residual indices, there are various other linear regression methods for bivariate data, depending on the parameters that are minimized (Ricker 1984, Rayner 1985, Martin and Barbour 1989, Harvey and Pagel 1991, Sokal and Rohlf 1995). In order to produce a meaningful index of condition, the slope and intercept of the fitted line should reflect the functional relationship between Y and X. Thus, the problem of line-fitting to calculate residual indices of condition is equivalent to the problem of establishing the allometric (or scaling) relationship between Y and X (LaBarbera 1989, Martin and Barbour 1989, Harvey and Pagel 1991).

As has been explained in detail by others (e.g., Ricker 1984, Rayner 1985, McArdle 1988, LaBarbera 1989, Martin and Barbour 1989, Harvey and Pagel 1991, Herrera 1992, Mesplé et al. 1996), the OLS method cannot be strictly appropriate to studies of body condition because this ''model I regression'' assumes that the values of the variable X are fixed by the researcher. In particular, the OLS method makes the assumptions (5) that X is strictly independent of Y and (6) that there is no ''error'' in X (i.e., that the scatter of points around a best-fit line is due entirely to variation in Y, not in X).

In studies of condition, body mass is always selected as the Y variable, yet in this case, assumption 5 is violated and X and Y are mutually interdependent. Indeed, body mass is invariably chosen as the X variable in the scaling literature (e.g., Boag 1984, Petrie 1988, LaBarbera 1989, Silva 1998; see also Badyaev et al. 1998: Fig. 1). Switching X and Y radically changes the position of the OLS regression line (Fig. 1). Likewise, the assumption (6) that there is no ''error'' in X (BSI length) is also violated in studies of condition. Inevitable measurement error (Yezerinac et al. 1992) is one source of this ''error,'' and BSI length may be subjected to higher instantaneous measurement error than mass (Krebs and Singleton 1993). An additional component of ''error'' in X comes from the unreliability of BSI length as a measure of structural size (i.e., shape variation).

Because of the violation of assumptions 5 and 6, OLS methods are biased: they fit lines in which the slopes tend to be underestimated (i.e., OLS slopes tend to be lower than those of the functional relationship between Y and X). This makes OLS methods ''inappropriate for most ecological applications requiring accurate estimates of regression parameters'' (Herrera 1992:1838). The use of ''model II regression'' is often likely to be more appropriate to studies of body condition. The two well-known model II methods are major axis and reduced major axis (RMA) regression. RMA assumes that the ratio (denoted by λ) of the error variance in Y

to that in X equals the ratio of the underlying true variances in Y and X. The major axis method assumes $\lambda = 1.0$, whereas OLS assumes $\lambda^{-1} = 0$ (assumption 6). These are all special cases of the structural relations model, which requires λ to have a known value (Rayner 1985, Harvey and Pagel 1991).

In the absence of a method for calculating λ (which is not available in studies such as those of Table 1), neither of the model II methods provides a perfect solution (Rayner 1985). However, RMA is considered more appropriate when Y and X are measured in different units (as in our case), and is more robust to violations of its assumptions about λ (Ricker 1984, McArdle 1988, Sokal and Rohlf 1995; but see Jolicoeur 1990). Both the error variance and the true variance in body mass can be expected to exceed their respective values for BSI length (Rising and Somers 1989). This suggests that the major axis assumption is untenable for regressions of mass on BSI length, and will lead to inflated slopes that may approach the OLS slope of X on Y (for related regressions involving body mass, see Pagel and Harvey 1988, Harvey and Pagel 1991).

Thus, RMA is often likely to be the most suitable alternative to OLS for calculating mass/BSI residual indices (for statistical methods, see McArdle 1988). RMA and major axis regression are both standard techniques in the scaling literature (e.g., Boag 1984, Herrera 1992, Simmons and Scheepers 1996, Silva 1998, Green 1999). RMA lines have the advantage of being easy to fit, because the slope is equal to the OLS slope divided by the correlation coefficient r, and the line passes through the centroid (the mean value of X and Y). RMA residuals are measured as deviations from the fitted line along the Y axis.

Ormerod and Tyler (1990) are the only authors from Table 1 who calculated mass/BSI residuals using model II methods. However, having found an inevitable correlation between these and OLS residuals, they proceeded to use the OLS residuals as a condition index. When r between Y and X is equal to 1.0, there is no difference between model I and model II regression lines. However, the lower the value of r, the greater the biases in OLS slopes and OLS residual indices are likely to be (LaBarbera 1989, Harvey and Pagel 1991, Green 1999). The values of r for tarsus or wing (in birds) or length (in mammals) against mass are often lower than 0.5 (Petrie 1988, Cavallini 1996, Gosler et al. 1998). Thus, these biases are likely to be large and important. The mean r between wing and mass for 51 passerine species was 0.34, and was lower between tarsus and mass (Gosler et al. 1998). Lower values of r between mass and the BSI tend to occur when the BSI is weakly correlated with other linear measures (i.e., when it is a poor indicator of structural size; Iskjaer et al. 1989).

In most studies of condition, r between mass and the BSI and other details of the OLS regression are not presented (Table 1), making it impossible to assess the potential for bias. In general, r values are higher in reptiles, typically exceeding 0.8 (see Table 1 and Forsman and Lindell 1991, Weatherhead and Brown 1996, Díaz-Paniagua et al. 1997), suggesting that OLS residual indices are more likely to be reliable for reptiles than for birds and mammals. However, Doughty (1996) found an r of only 0.29 between SVL and mass in the gecko *Gehyra variegata.*

When λ is more than the ratio of the true variances in Y and X, the slope best representing the functional relationship between Y and X lies between the RMA and OLS lines. OLS methods can be less biased than RMA methods when λ is more than three times the ratio of the true variances in Y and X (McArdle 1988, Sokal and Rohlf 1995). This is conceivable for some studies, because mass is subject to high temporal variability in relation to such organismal characteristics as feeding, metabolism, and excretion. However, this view is partly encouraged by the misunderstanding that measurement error is the only source of ''error'' in X. Variation in the extent to which BSI length accurately represents structural size (i.e., shape bias) is another major source of this ''error.'' Body mass can be less variable over time than many other measures (Ots et al. 1998), and correcting for ingesta mass makes almost no difference to the value of OLS residuals as a condition index (Cavallini 1996, Weatherhead and Brown 1996).

A strong relationship between r values and OLS slopes tends to confirm that the latter are biased (Green 1999). In their study of condition in Dippers *Cinclus cinclus* (Ormerod and Tyler 1990), OLS slopes (after log transformation, equivalent to allometric exponents) of mass on wing or tarsus ranged from 2.02 (when r was 0.77, pooling all birds together) down to 0.24 (when r was 0.09, analyzing age classes and sexes separately). In contrast, the corresponding RMA slopes remained stable within a realistic range, changing from 2.62 to 2.68. The functional relationships between body mass and wing or tarsus (in bird populations) or body length (in mammal or reptile populations) tend to have an allometric exponent lying between 2.5 and 3.2, close to the value of 3 expected under simple geometric scaling (Boag 1984, Petrie 1988, Bradshaw and De'ath 1991, Krebs and Singleton 1993, Green 2000).

A study of the mass/tarsus relationship in Greater Flamingo *Phoenicopterus ruber* chicks provides another example of how OLS slopes are lower as r decreases. Variation in the OLS slope (range 1.150–1.687) of log mass against log tarsus length between eight years was almost perfectly explained by variation in r (Cézilly et al. 1995: Table 1). The equivalent RMA slopes were less variable between years (range 1.730–1.958; note that values well below 3 reflect the rapid leg growth of flamingo chicks). Lower r values reflected years of lower water levels and poorer feeding conditions, which appear to increase variation in the mass/tarsus relationship.

In no previous study using OLS residual indices (Table 1) is enough information presented to allow the recalculation of mass/BSI residuals via model II regression. In future studies of condition, more detail should be presented on the regressions and residual calculations, to enable an assessment of the extent to which the results are sensitive to the method used (see LaBarbera 1989 for details that should be presented in line-fitting exercises).

When OLS methods underestimate slopes, they tend to inflate residuals with increasing BSI length (i.e., structurally larger individuals tend to have relatively higher residuals). In many of the studies in Table 1, the parameters that correlated significantly with OLS residuals are also likely to correlate with structural size. Hence, the significant effect of the residuals is potentially a statistical artifact of a relationship between the parameter and structural size, not ''condition.''

This problem is particularly serious in those studies in which OLS residual indices are related to the size of characters used in courtship or competitive display (Andersson 1992, Carranza and Hidalgo 1993, Veiga 1993, Mateos and Carranza 1996, Cordero et al. 1999), because such characters are likely to be strongly correlated with structural size (e.g., Petrie 1992, Simmons and Scheepers 1996). However, many of the other parameters correlated with OLS residuals (Table 1) could also be related to structural size. Thus, in a given population, structurally larger birds or reptiles may lay larger eggs (Potti 1993, Díaz-Paniagua et al. 1996, Doughty 1996, Dufva 1996), may have a larger clutch (Ford and Seigel 1989, Sedinger et al. 1995, Madsen and Shine 1999), or may have an earlier laying date (Díaz-Paniagua et al. 1996, Winkler and Allen 1996, Cuadrado and Loman 1999). They may provide room to house more parasites or show different levels of aggression. Equally, structurally larger mammals may breed earlier (Dobson and Michener 1995, Birgersson and Ekvall 1997) or may produce heavier litters, and larger reptiles may move a greater distance each day (Díaz-Paniagua et al. 1995).

When using OLS residuals as a condition index, one can expect Type II errors in cases where the residuals are analyzed against a parameter that is related to true body condition, particularly when r is low. In male Red-legged Partridges *Alectoris rufa,* correlations between mass/tarsus residuals from OLS regressions and the concentration of plasma carotenoids (potentially an important physiological indicator of condition; Olson and Owens 1998) were not significant. However, these correlations were significant using RMA residuals (r between mass and tarsus = 0.39; Negro et al., *in press*).

An Example of How OLS Residuals can Produce Statistical Artifacts

I illustrate the ease with which artifactual relationships and Type I errors can be generated by OLS residuals using the morphometric data from 198 male Green-winged Teal (*Anas crecca*) measured in their first year of age in 1984 at Abberton Reservoir, United Kingdom, by Fox et al. (1992). Using OLS and RMA methods for comparison, ln body mass was regressed on ln tarsus length ($r = 0.233$). Prior investigation with nonparametric regression (cubic spline in the S-Plus [2000] package) confirmed that there was no significant deviation from linearity in the relationship ($P > 0.2$). For the reasons previously given, an OLS regression of Y on X produced an excessively shallow slope ($b = 0.73$), whereas an OLS regression of X on Y produced an excessively steep slope ($b = 13.4$; Fig. 1). When the dependent and independent variables are interchanged, all those birds lying between the two OLS lines in the upper right part of the plot switch from being relatively heavy for their tarsus length to having a relatively large tarsus for their mass (and vice versa for the birds on the lower left of the plot). This is contradictory, and further illustrates the unsuitability of OLS methods. The RMA slope is 3.12 (Fig. 1) and, unlike the two OLS slopes, is not significantly different from 3, the value expected under simple geometric scaling (note: the position of the model II line does not depend on whether mass is Y or X).

Residuals were calculated from the OLS regression of ln mass on ln tarsus (i.e., from Fig. 1). These OLS residuals were then correlated against a separate measure of body size for each individual, that of ln maximum skull length. A highly significant correlation was found ($r = 0.258$, $P < 0.001$; Fig. 2). This is a result equivalent to those of many studies from Table 1, and an extension of logic applied therein would suggest an important correlation and causal relationship between body condition and head length in Green-winged Teal.

However, this result is a statistical artifact resulting from the biased residuals from OLS regression. The OLS regression of Y on X inflates the residuals in teal with larger than average tarsi and reduces them in teal with smaller than average tarsi (Fig. 1). For comparison, residuals were calculated from the RMA regression of mass on tarsus (from Fig. 1), as observed minus fitted Y (ln mass). As expected, the RMA residuals were not significantly correlated with skull length ($r = 0.06$, $P > 0.4$). Both the OLS (Shapiro-Wilks' W test for normality, $W = 0.980$, $P = 0.35$) and RMA residuals ($W = 0.979$, $P = 0.27$) were normally distributed, although the RMA residuals had a higher standard deviation (0.125) than the OLS residuals (0.098) because, by definition, OLS minimizes the sum of the squares of the residuals. The RMA and OLS residuals were highly correlated ($r = 0.785$, $P < 0.001$). As anticipated, major axis regression produced an inflated slope (12.1) similar to the OLS slope of X on Y.

Similar results were obtained with a sample of 127 female Green-winged Teal of the same age, measured at the same time (Fox et al. 1992). Again, ln skull length was significantly correlated with OLS residuals of ln

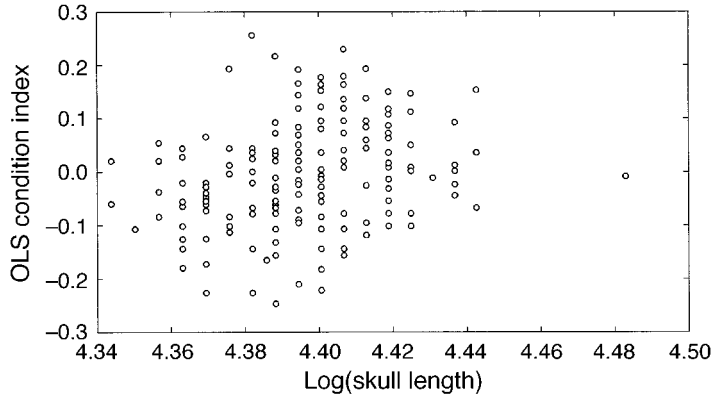

FIG. 2. Residuals from the OLS regression of Y on X (from Fig. 1) against skull length in male Green-winged Teal ($N = 198$; $r = 0.258$, $P < 0.0003$).

mass on ln tarsus ($r = 0.224$, $P < 0.012$), but not with RMA residuals ($r = -0.165$). Similar examples of artifacts are easily generated from other avian morphometric data sets.

On Lack of Fit in OLS Regression

When there are repeated runs in the data (multiple Y values for each value of X, from different individuals and *not* from repeated measurements of the same individual), it is possible to divide the residual sum of squares (SS) in an OLS regression into ''lack of fit'' SS and pure error SS (Draper and Smith 1998). If the mean squares because of lack of fit is significantly greater than the pure error term, the fitted model is inadequate and should not be used to calculate residuals. For example, in Fig. 1 there are repeated runs of ln mass for each value of ln tarsus, but the lack of fit is not significant (analyzed in JMP package, SAS Institute [1995]: $F_{11\,185} = 1.12$, $P > 0.34$).

However, this repeated-runs analysis makes the same assumptions (5 and 6) as other OLS methods, so that if a fitted model passes this test, it is still likely to underestimate slopes and produce biased residuals. Thus, if we reverse axes and regress X on Y in Fig. 1, the lack of fit is again nonsignificant ($F_{30\,166} = 1.13$, $P > 0.31$). Therefore, such an analysis does not confirm that the OLS line reflects the functional relationship between Y and X as required (although a significant lack of fit confirms that it cannot).

On Correlations between Residuals and the X Variable

With OLS regression, the resulting residuals have a zero correlation with observed X, but are positively correlated with observed Y. An important property of the RMA regression is that the resulting residuals have correlations of equal magnitude with both observed X (negative) and Y (positive). The zero correlation between OLS residuals and BSI length has previously been cited as an important advantage of OLS residuals as a condition index (Reist 1985, Jakob et al. 1996). This argument is dependent on assumption 3 that the BSI is an accurate indicator of true structural size. Correlations between model II residuals and X are likely to be a reflection of ''error'' in X, because higher BSI lengths are more likely to overstate structural size (owing to measurement error and shape variation), whereas lower BSI lengths are more likely to understate structural size. Extreme data points are liable to be the more poorly estimated ones (Link and Sauer 1996). An appropriate test to see if residuals are independent of structural size is to check if they are correlated with separate size measures (i.e., alternative BSIs). Zero correlations are desirable, and significant correlations confirm that the residuals are biased (recall the teal example). The regression method with mass/BSI residuals showing the lowest correlation (in magnitude) with separate size measures is likely to be the least biased and most appropriate for that study.

Where there is a sound basis a priori to define the allometric relationship between mass and the BSI, an acceptable alternative for calculating residuals for a condition index would be to force this scaling line through the centroid. This may be a useful approach in cases where r is very low (e.g., below 0.1), when RMA slopes become unreliable. However, where r approaches zero, body mass itself may be a better index of condition than any residual.

Conclusions

A series of key assumptions underlying the current fashion to use OLS residuals of mass on BSI length as an index of condition has been identified (see also Kotiaho 1999). Each of these assumptions is likely to be violated in some recent studies. The frequency and consequences of the violation of these assumptions may explain why OLS residual indices are poorly correlated with the relative size of fat stores and other direct measures of condition (Conway et al. 1994, Cavallini 1996, Weatherhead and Brown 1996). No significant relationship has been observed between OLS residuals and body fat content in house mice *Mus domesticus* (Krebs and Singleton 1993) or muskrats *Ondatra zibethicus* (Virgl and Messier 1993).

I suggest that the errors in the residuals used as an index of body condition can be sufficiently great as to leave the results of some previous studies (Table 1) open to question. In the future, more care is advisable when using and interpreting residual indices. The tendency to use the word ''condition'' (without the word ''index'') as a synonym for mass/BSI length residuals in many studies in which no comparison is made with more direct measures of energy stores (Table 1) is precipitative, potentially misleading, and best avoided.

It is difficult to interpret the relationship that any index computed merely from measures of mass and size has with true physiological condition or the relative size of energy stores (Ormerod and Tyler 1990, Dobson and Michener 1995, Brown 1996). Unfortunately, no mass/BSI residual indices are likely to have a very strong relationship with direct measures of condition (see Johnson et al. 1985, Spengler et al. 1995, Winstanley et al. 1998). However, nondestructive indices of body condition are obviously a useful and necessary tool in ecology. Various ways of improving these indices have been identified here.

Repeated measurements of the BSI should be made to increase its accuracy (Yezerinac et al. 1992). PC1 from a PCA of multiple measures of structural size should be used more often as a more reliable BSI than individual measurements. Alternatively, residuals could be calculated from a multivariate model that includes mass as the dependent variable and each size measure as a separate predictor (see McArdle 1988 for the RMA equivalent of OLS multiple regression). In some studies, PC2 from a PCA of various linear size measures plus body mass may be a useful index of that part of body mass which is independent of structural size (Dobson 1992), although this needs to be investigated on a case by case basis. It is not always appropriate to include mass in a PCA of size measures, and in such cases, PC1 can be influenced by condition (Alisauskas and Ankney 1990, Piersma and Davidson 1991).

The aim of this paper is not to replace the current orthodoxy of the universal validity of OLS residuals with another orthodoxy of RMA residuals. A more flexible and cautious approach is required, given the scale of the problems with such residual indices. The reliability of RMA residual indices is reduced by violations of assumptions 1–4, as well as by the RMA assumption about λ. Like OLS, RMA lines can easily misrepresent a functional relationship between mass and body size (Pagel and Harvey 1988, Lindström and Piersma 1993, van der Meer and Piersma 1994).

Assumptions of linearity should be tested in each study, and nonparametric regression should be used to produce residual indices when the functional relationship between mass and BSI (following any transformations) may be nonlinear. When assumptions of linearity are not violated, the line best reflecting the functional relationship between Y (mass) and X (BSI length) is often likely to lie between the RMA and OLS lines. It would therefore be prudent to compare the effects of OLS and RMA methods in each study using residual indices, thus testing the sensitivity of residual indices to different methods. Great care should be taken in interpreting results that differ between the two methods. This interpretation will be aided by correlating BSI length and mass with the parameter of interest. For example, if only OLS residuals correlate significantly with a given parameter, and BSI length also correlates significantly with this parameter, there is no reasonable evidence that the former is based on an effect of ''condition.''

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